HOLARCTIC LANDMASS REARRANGEMENT, COSMIC EVENTS, AND CENOZOIC TERRESTRIAL ORGANISMS

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Abstract

Rearrangement of landmass configurations has profoundly affected the evolution of mammals and other organisms in the Northern Hemisphere. At the north end of the Atlantic Ocean, evidence is very strong for a now sundered landmass of Euramerica. This landmass existed toward the end of the Paleocene but began to separate into at least two landmasses in early Ypresian time at the beginning of the Eocene. Throughout most of the Eocene, Western Europe south of the Baltic Sea remained fragmented and separate from both Asia and the part of Europe and the attached Barents Shelf that lies north of the Baltic. Northern Scandinavia may have been essentially a peninsula of North America until the end of Eocene time. Thus at the end of the Paleocene and until some point very early in the Eocene, *two* land bridges may have simultaneously connected North America with separate parts of Europe across the north end of the Atlantic: one dominated by compression in the Greenland/Svalbard area plus any excess lava pile generated by early activity of the Yermak hotspot northwest of Spitsbergen, the other by the early activities of the Icelandic hotspot. Possibly a connection from western Asia and Europe to the northeastern end of North America existed at about 37 million years ago (Ma) through the combined activities of the Yermak hotspot, waning compression between Greenland and Svalbard, and the drying of Eurasian seaways. Throughout nearly all of the Cenozoic a land connection between Asia and Alaska existed at the Bering Strait, but the paleolatitude of the Bering Bridge was initially high and climate must have exerted a strong filtering action on mammals and other terrestrial organisms. It is possible, but only weakly supported on geological grounds, that a second northern Pacific bridge between Asia and North America existed via the Aleutians at the time the Kula Ridge was subducted. Other rearrangements that have strongly affected the composition of northern mammalian faunas and presumably would have affected many other organisms as well have been the reconnection of South America to North America in the Pliocene, the collision of India with Asia in the early Cenozoic (possibly earlier), and various Tethyan microplate transfers. Although paleobotanists and others have sometimes suggested that the warm polar climates of the early Cenozoic were the result of a lower mean spin axis obliquity of the Earth than the present 23.5°, no one has explained adequately how mean spin axis obliquity can be permanently changed significantly in the Cenozoic, where the necessary force would come from to shift it, how such a force would be coupled to the Earth, or how the resulting crustal heat would be dissipated. At present, therefore, known high latitude early Cenozoic environments of mammals and other organisms are not well understood, but a significant change of Earth's mean spin axis obliquity since the early Cenozoic is evidently out of the question. A catastrophic theory of Apollo-class asteroid impact at supposedly 35 Ma has recently been invoked to explain major Eocene/Oligocene faunal turn-over. However, major turn-over in both the marine and terrestrial realms occurred well before 35 Ma in both Europe and North America, as did the "North American tectite strewn field." Several such fields exist, however. Under a stable continent rationale, concepts of corridors, filters, and sweepstakes routes were developed by the 1950s by G. G. Simpson. Under a mobile continent rationale additional paleogeographic concepts have been added since then, such as Noah's arks and grounded Viking funeral ships for colliding or coalescing terranes bearing respectively either living or fossil contents. In addition, vicariance biogeography, with its emphasis on congruent cladograms of both the genealogies of the biota and of the geologic history of various areas, has been born and is undergoing growing pains. To these concepts may be added the notions of escalator counterflow and escalator hopscotch, whereby the existence of archaic elements of a biota can be reconciled with their presence on young mid-ocean-ridge islands like Iceland or mid-plate volcanic edifices such as those of the Hawaiian-Emperor chain. The retreat from, and return to, continental coasts by island arcs affected by subduction zone jumps provides a geological mechanism for biological voyages to nowhere and return, as would happen if the landmass of the volcanic arc separated from its parent continent, remained for a while in isolation, and then once more contacted the continent. Vicariant biotas produced by such means and nurtured in isolation would thus eventually be passively returned to contiguity with the parent continent. A certain amount of caution is called for before one should invoke far-traveled tectonic blocks, such as those plastered against the present shores of the North Pacific, as carriers of vicariant biota, now endemic to a terrane embedded in a foreign land. Before accepting such a block as a possible carrier of a terrestrial or even shallow water marine biota, it is important to determine if the block possesses continental or oceanic tectonic basement. Was the surface of the block always above sea level? Were its organisms transported only

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as fossils? Are the proposed vicariant sister groups at reasonable taxonomic levels in view of the time of tectonic transport of the block while in isolation? A parsimonious approach to all natural history, not merely biology, is necessary. Ad hoc hypotheses should be held to a minimum. The expanding Earth hypothesis is discounted as an explanation of discernible late Phanerozoic biogeographic pattern. Studies of mammalian diversity based on the fossil record have often been biased by tacit assumptions that biostratigraphic units have represented aliquot divisions of time. Calibration of mammalian biostratigraphy is under way, but until the subject is more advanced, published diversity/time relations should be taken with a grain of salt.

Authors of invited papers like this one are usually given the title of their paper, covering subject matter that the symposiarch hopes will somehow be dealt with adequately. However, the task usually proves to be overwhelming and the beleaguered author, nearly always at the last minute, produces instead a manuscript entitled "Problems of such and such." The author is then off the hook and able to postpone the real work. The "definitive effort" can always be written sometime next year. However, this paper is frankly such a preliminary effort even though it is longer than I would like it to be. In it I try to get at some of the main points in a vast subject in which I have taken some interest over the years, but it is aimed at an audience whose knowledge of vertebrate paleontology or modern geology is not necessarily very extensive and who might find a documented review useful. To me it seems obvious that some of the physical changes in the world that either have or might have affected the distribution of mammals in both space and time would also in some way affect much of the rest of the planet's biota. Our world has had a single history, which we try to decipher from a mixture of signal and noise coming from many sources of potential evidence. With regard to spatial distribution, the signal has in part been generated by geological processes and the noise in part by biological random dispersal and sampling errors. Although what follows is primarily a distillation from geology and mammalian vertebrate paleontology, the consequences are testable within other fields, such as botany and non-mammalian zoology. Indeed, the biological data can be used to test geological notions about the position and timing of continental interconnections, epicontinental seaway barriers, and so on. Geologists have much to learn from biologists, provided that the formulations of the biologists are well-founded.

A MOBILE GARDEN OF EDEN

Early attempts to discuss the relationships of the vertebrates of the Northern Hemisphere, like those concerning plants or invertebrates, were necessarily based on the living biota alone and were made on the assumption that the geography of the Northern Hemisphere has always been more or less the same as it is now, give or take a seaway here or there, a shift in a coastline, or a cyclic change in climate (Dana, 1847, 1863). The Sclaters' (1899) and other nineteenth century authors' realms, regions, and so forth were based on such a foundation (de Beaufort, 1951; Simpson, 1953, 1965; Uvardy, 1975; Nelson & Platnick, 1981).

Gradually, however, the richness of the Recent data has been supplemented by an increasing knowledge of the vertebrate fossil record of various parts of the Earth. The geologic history of the world, in part dated by the fossil record and in part dated by other means, has become increasingly well known, spectacularly so in the last few years of intense effort associated with the plate tectonic revolution in geology.

But our paleontological knowledge of fossil vertebrates has not grown uniformly or smoothly. Indeed, the way our knowledge has grown has caused a bias in the results, partly because of the apparent randomness of discovery and partly because the efforts have largely emanated first from Europe, then from America, and finally from Asia and northern Africa. Thus, as time has passed, perspectives have shifted radically. At first, Europe was taken as an adequate sample of Holarctica. The evolution of horses, for instance, was believed to be a continuity represented in the European record by Eocene *Palaeotherium*, Miocene *Anchitherium* and *Hipparion*, and finally Pleistocene and living *Equus* (Huxley, 1872; Kowalevsky, 1873). However, the principal scene of equid evolution was elsewhere and the European record is now seen to be discontinuous, the result of repeated immigration to Europe of closely related animals rather than the product of our sparse temporal sampling of a single indigenous evolving lineage. Much the same may be said of camels, elephants, rhinoceroses, and many other groups of mammals.

Important as the European record was (and still is) for deciphering the Cenozoic vertebrate record of Holarctica, it suffers from several profound defects. For instance, there is no record of terrestrial Tertiary fossil tetrapods anywhere from the whole Fennoscandian northwest end of Europe, an area including Sweden, Norway, and the formerly subaerial Barents Shelf that lies in the Arctic between them and Svalbard. Another difficulty with the European Cenozoic record is that, until very recently (Godfriaux & Thaler, 1972; Thaler, 1977; Vianey-Liaud, 1979), there has been no record of medial or early Paleocene terrestrial vertebrates in Europe.

Starting in the 1870s, an explosive phase in the geological and paleontological exploration of the North American West began. This work soon produced an apparently much more continuous view of the evolution of various mammalian groups than had come to light in Europe other than for obvious European endemics such as doormice, certain kinds of artiodactyls, or dimylid insectivores, to name a few random mammalian examples. In North America, furthermore, terrestrial Paleocene sedimentary rocks turned out to be more completely represented than in Europe. Until recent discoveries, the terrestrial early or medial Paleocene fauna was represented solely in North America, where the land-laid deposits of the Rocky Mountain area of the United States and Canada supplied abundant and fairly well preserved fossil remains representing the earlier parts of the Paleocene. It was natural, then, that this North American terrestrial Paleocene sequence of faunal assemblages came to be regarded tacitly as representative of the ancestry of younger faunas on many continents, just as Europe had once been regarded as such a source. The Cenozoic Garden of Eden had shifted from Paris, France, to western North America, never to return.

But as the North American terrestrial vertebrate record was filled in by the efforts of E. D. Cope, O. C. Marsh, W. D. Matthew, and their successors, several important discontinuities appeared and some biogeographically disturbing alliances began to loom. Although a much more continuous record of certain groups, such as the famous horse sequence, was established in North America, a break between the American Eocene and Oligocene became obvious from the mammalian record (Wilson, 1980). Also, the source of several floods of latest Paleocene and/or early

Eocene immigrants (Rose, 1981) into known fossil-producing areas of both North America and Europe from somewhere else became an increasingly vexatious problem. Furthermore, known North American late Cretaceous therian mammals did not appear to be ancestral to most Cenozoic forms.

For these reasons, northern Asia came to be regarded as the likely true Garden of Eden, where, if the record of remote Central Asia could just be sampled, all would become clear. Professor Henry Fairfield Osborn of Columbia University and the American Museum of Natural History held the firm belief, as did most of his associates, that the northern Asian ("Central Asian") record held the answers to the origin of various northern groups, including our own ancestry among the higher primates (Osborn, 1923a, 1923b). Osborn's view was responsible in large part for the mounting of the Central Asiatic Expeditions, a series of explorations in China and Mongolia that held the scientific spotlight in the field of natural history in the 1920s and whose spectacular labors filled in for the first time much of the Cretaceous, Eocene, Oligocene, and late Miocene terrestrial history of Mongolia and northern China. In Central Asia Osborn expected to find the ancestors of various rootless lineages of vertebrates known from Europe and North America. Given the assumptions of a stable-continent framework that prevailed in North American paleogeography in those days, what could be more natural than to find such links on the geographically intermediate landmass of Asia, half way between North America and Europe?

Early Cenozoic Holarctic Rearrangement

But, the northern Asian record for the early Cenozoic turned out to be a disappointment for ancestor seekers. Instead, as so often happens in science, a whole new series of problems arose (Szalay & McKenna, 1971; Fox, 1978). In place of ancestors, the Mongolian and Chinese early Cenozoic in many, even most, instances produced a new endemic cast of characters wholly unexpected in the terrestrial deposits of what was supposed to have been a continuous corridor (Simpson, 1943, 1953) connecting North America across Asia all the way to Europe. More recent collecting in the Paleocene of China has lent an even more peculiar aspect to early southeastern

Asian terrestrial faunas (Li & Ting, 1983). For instance, early primates, common enough in the North American and European Paleocene, are thus far completely absent from the Chinese Paleocene with only one possible but disputed exception, *Petrolemur*. Primates apparently reached eastern Asia only at the very beginning of the Eocene (Dashzeveg & McKenna, 1977). Multituberculates are also totally unrepresented in the known Chinese Paleocene, although they were previously abundant in the Mongolian Cretaceous and occurred again in Chinese and Mongolian assemblages at the very beginning of the Eocene. In place of these primates and multituberculates, Chinese Paleocene faunas supply us with a flood of new taxa that most Western paleontologists have found bewildering in variety and difficult to place in the scheme of things. In facile retrospect, clearly something was wrong and the flaw surely could have been spotted in the 1920s or 1930s had not the stable-continent rationale prevailed (Simpson, 1953, 1965).

What I refer to, of course, is that landmass interconnection within Holarctica in the early Cenozoic was arranged a bit differently from the familiar geography of the present day and of the Pleistocene (Wolfson, 1949; Nelson, 1973; McKenna, 1983). In the early Cenozoic, western Europe south of the Baltic Sea area and also the Fennoscandian shield of northwestern Europe north of the Baltic were for a time separately connected to North America by parallel routes around the north end of the Atlantic Ocean. Geological and paleontological evidence is more consistent with this reconstruction than one favoring an indirect connection by way of continuous land from northwestern North America to eastern Asia and then from western Asia to various parts of Europe. A continuous and habitable land connection from France and the British Isles to America via the Greenland-Scotland Ridge was a reality in the late Paleocene and earliest Eocene; most of the route, as far east as Iceland, may still have been intact above sea level as late as the Miocene (McKenna, 1975, 1983) although at least one break in land continuity must have been present as early in the Eocene as some point in Ypresian time. North of the Greenland-Scotland Ridge, a second connection between Greenland and Fennoscandia may have been possible throughout much of the Eocene because of compression between Svalbard and Greenland during the Eocene (Lowell, 1972) and possibly because of the early activity of the Yermak hot-spot beginning at about 40 million years ago (Ma) (Batten et al., 1981).

Meanwhile, Asia was difficult to reach directly from North America or vice versa, not because of the lack of a land connection, but because the ancient land continuity between northeastern Siberia and Alaska was then at very high paleolatitudes (Wolfson, 1949). Until the end of the Eocene, marine barriers existed between central Asia and *western* Europe south of the Baltic, preventing terrestrial organisms of France, England, Belgium, Spain, and Portugal from reaching Asia from the west and forcing any dry-land dispersal of such forms in the late Paleocene or early Eocene to take place via the Greenland-Scotland Ridge, the eastern Arctic, and the north shore of the Pacific by way of Alaska and eastern Siberia. Russian authors have sometimes claimed that the Turgai Strait broke down in the early Eocene and permitted Eurasian transfers to take place via the so-called Kustanai elevation (Novodvorskaja & Janovskaja, 1977) at the narrowest part of the Turgai Strait, but this connection, if it existed, would not have been a route connecting western Asia directly to western Europe south of the Baltic. Rather, a Turgai Bridge at the Kustanai elevation in the early Eocene would have connected Asia directly to Fennoscandia, from whence terrestrial organisms may have been able to reach the rest of the western Europe via a round-about dry-land route through Greenland and proto-Iceland. Dispersal in the opposite direction over the same route might have occurred as well. In the mid-Tertiary, southwestern Asia was apprently isolated from Europe (Jacobs et al., 1981; Heintz & Brunet, 1982).

The effects on the biota of this formerly very different geography of the northern world are profound, although even now they are not well understood. No longer, however, can it be said as, for instance, Darlington (1957: 606–607) did, that fossil mammals support the notion of permanent continental allegiances and permanent oceanic barriers. Rather, patterns of endemism shown by early Cenozoic Holarctic mammalian faunas are consistent with the paleogeography reconstructed by students of plate tectonics (McKenna, 1975, 1983).

THE EARLY CENOZOIC POLE POSITION

I have elsewhere summarized the rather scanty published data bearing on the position of the early Cenozoic rotational pole with regard to

TABLE 1. Position of early Cenozoic rotational pole with regard to North America (from McKenna, 1980a).

Age	Latitude N.	Longitude E.	Error	Author
60 Ma	75.9°	147.7°	—	Butler and Taylor, 1978
45 Ma	87°	169°	6°	Simpson and Cox, 1977
45 Ma	82°	170°	5°	Irving, 1979

TABLE 2. Position of early Cenozoic rotational pole with regard to North America (from Harrison & Lindh, 1982a, 1982b).

Median Age	Studies	Latitude N.	Longitude E.	Error
76.3 Ma	11	70.6°	195.1°	7.4°
67.9 Ma	18	76.6°	188.4°	5.6°
58.5 Ma	23	80.0°	183.8°	4.7°
48.3 Ma	26	83.1°	178.2°	3.5°
38.9 Ma	26	83.4°	165.4°	3.5°
30.4 Ma	29	84.7°	157.7°	3.6°
19.9 Ma	25	85.9°	151.1°	3.6°

North America (McKenna, 1980a). Various previous calculations yielded the results shown in Table 1.

Recently, these results have been upgraded by Harrison and Lindh (1982a: 1912, table 8; 1982b), utilizing a carefully conceived method of averaging and weighting data. Their results for a period covering the interval from about 80 to 20 Ma are shown in Table 2.

Harrison and Lindh (1982a) made a concerted effort to avoid inclusion of paleopolar data from displaced terranes of Western North America (Beck, 1980; Cox, 1980). Their results differ significantly concerning the 40 Ma paleopole of Briden et al. (1981), but the latter included data from the almost certainly rotated Twin Sisters dunite of the state of Washington (Beck, 1975). Harrison and Lindh removed the Twin Sisters dunite data and, using the method of Briden et al., obtained results close to their own (Harrison & Lindh, 1982a: 1910).

Thus, in the middle of the Eocene the averaged magnetic pole position, or in other words the position of the Earth's rotational axis, was relatively about 7° closer to the Bering Strait area than at present. Put another way, since the medial Eocene the lithosphere in the Bering area has moved away about 7° relative to the mean position of the Earth's spin axis.

It is also important to know the paleolatitude of Ellesmere Island in the early Cenozoic. Eocene fossil invertebrates, vertebrates, and deciduous plants are now known from that critical area of the northeastern Canadian high Arctic (Miall, 1981; West et al., 1981) and therefore these organisms yield information about the early Cenozoic environment there. At the time or times in the early Cenozoic when these organisms were capable of living on Ellesmere Island, the world's oceans were quite warm (Savin et al., 1975; Savin, 1977; Buchardt, 1978; Shackleton & Boersma, 1981) and poleward transport of heat by

oceanic currents and the atmosphere was evidently great. Ellesmere Island was at that time almost certainly located on the path between Canada and either of two bridges that separately connected Greenland with lands to the east. The paleolatitude of terrestrial Eocene fossil vertebrate-producing sites on Ellesmere Island, whose present coordinates are here taken for convenience as 78.75°N, 277.25°E, can be recalculated for 48.3 Ma using the following formula:

$$\text{Paleolat.} = \sin^{-1}[\sin \text{lat.}_s \sin \text{lat.}_p + \cos \text{lat.}_s \cdot \cos \text{lat.}_p \cos(\text{long.}_p - \text{long.}_s)].$$

In this formula, s = site and p = position of former rotational pole.

Such a calculation yields a medial Eocene paleolatitude for the terrestrial fossil-bearing sites: 75.9°, error 3.5°. This result is not significantly different from my previous paleolatitude calculation for the Ellesmere sites: 77.5°, error 6° (McKenna, 1980a), nor from their present latitude. If the paleopole position for 48.3 Ma determined by Harrison and Lindh is accepted, then the Eocene Ellesmere Island terrestrial biota would have lived at an angular distance of 14.1°, error 3.5°, from the spin axis, well within the Arctic Circle if the extent of the Arctic Circle was then the same as now. The path of polar relative motion between the rotational axis position and that of the Bering Strait area was approximately at a right angle to a line from the pole to the Ellesmere sites. For this reason the paleolatitude of Ellesmere Island has not changed significantly during the Cenozoic, while that of the Bering Strait area has decreased by about 7° since the medial Eocene and by a total of about 13° since the end of the Cretaceous. Thus, in the early Cenozoic, the Bering area was relatively much closer to the rotational pole than the Eurameri-

can connections at the north end of the Atlantic Ocean.

Mean Obliquity of Earth's Spin Axis

Several authors, notably Allard (1948), Williams (1972, 1974), Wolfe (1977, 1978, 1980), and Xu (1980), have claimed on the basis of botanical and other indirect climatic evidence that the mean spin axis of the Earth was more nearly parallel to the axis of the Earth's orbit in the early Cenozoic than its current mean obliquity of 23°27'3". This would mean that the radius of the Arctic Circle has increased since the early Cenozoic. Such a notion is attractive at first glance because it would have permitted nearly equal days and nights throughout the year in those times and would not have fatally disrupted photosynthesis. But there is a problem with the physics of this hypothesis. Mechanisms exist, of course, for moving a large part of the Earth with respect to another oppositely moving part or parts (Gold, 1955; Goldreich & Toomre, 1969; Jurdy, 1981), but a large extraterrestrial force operating over a long time would be required to affect the angular momentum vector Hx of the entire Earth (Fisher, 1974: 4044). Except for orbital resonances that are not expected to affect Earth for another couple of billion years (Ward, 1982; Harris & Ward, 1982), no such enormous force capable of affecting Earth significantly in the Cenozoic is known. Moreover, were it to exist, no way is known to couple it to the Earth. The law of conservation of momentum stands in the way. Collisions with large, high-velocity comets or large, relatively low velocity asteroids would, of course, produce instantaneous effects as well as long-term ones, especially at very early times in the Earth's history (Clube & Napier, 1982), but by Cenozoic times such effects would have become negligible. An effect large enough to shift the axis instantaneously as much as 5° (Nafziger & Dachille, 1965) would have totally disrupted the life of our planet as well as its geology. Averaged over a long time, essentially random arrivals of large extraterrestrial bodies would affect the spin axis's orientation if enough such arrivals occurred. But if a long-term gradual shift of the mean obliquity of the Earth's spin axis with regard to the ecliptic had in fact occurred since the end of the Mesozoic, then one would expect that, in the much longer interval since the early Precambrian, the mean obliquity of the Earth's axis as well as those of most other large bodies in the solar system would have shifted so much that a random scatter of their mean inclination values would prevail. Such is not yet the case (McKenna, 1980a). Moreover, for the Earth at 850 Ma in the late Precambrian, obliquity calculated from growth features of stromatolites at one site was about 26.5° (Vanyo & Awramik, 1982), close to the present value and therefore evidence for long-term stability since the late Precambrian. True, only one site of that age has been investigated in this way so far, but the matter can easily be tested further.

One could also bring up the problem of how to dispose of the enormous amount of heat that would necessarily have been generated in a short time if a large extraterrestrial force was indeed applied rapidly, etc.

I am thus unconvinced by all indirect arguments claiming modification of mean obliquity with respect to the Cenozoic ecliptic that do not deal quantitatively with the required physics of the process (Ward, 1982). If empirical evidence of such an event were found, then physics would have to explain it, but thus far the arguments are indirect chains of reasoning based on conclusions about past climates that are in some cases themselves suspect.

From the preceding arguments I conclude that the Eocene climate of the areas where North America was connected to other northern landmasses was generally warm but necessarily seasonal, and that in general the North Atlantic connections would have been more hospitable than was the case at the north end of the Pacific.

The Grande Coupure

The Grande Coupure (Stehlin, 1909) is a strong break in western European faunal continuity that occurred between Ludian time (= Priabonian, latest Eocene) and Sannoisian time of the early Oligocene (= early Rupelian, Stampian, or Latorfian of some authors. See Bosma, 1974; Brunet, 1975, 1977; Cavelier, 1976; Cavelier et al., 1981; Hartenberger, 1983; Berggren et al., in press).

The western European terrestrial Oligocene fauna shows a major turn-over following the Eocene, with many mammalian extinctions and also many mammalian introductions from elsewhere, mainly from Asia and southeastern Europe after the drying-up of certain eastern European seaways and the former Turgai Strait (Obik Sea). The latter had until then formed an

epicontinental water barrier between Asia and Europe nearly continuously since the Jurassic (McKenna, 1975; Heissig, 1979). A sharp decline in oceanic bottom water temperatures throughout the world occurred at the same time (Kennett & Shackleton, 1976; Corliss, 1979; Keigwin, 1980; Cavelier et al., 1981; Norris, 1982). Thierstein and Berger (1978), as well as Miller and Curry (1982), have argued that this temperature drop was caused by recombination of previously isolated brackish Arctic Ocean water with that of the world ocean, a sort of latter-day reincarnation of the Gartner and Keany (1978, 1979; see also Clark & Kitchell, 1979) Arctic spill-over model in which cold, low-salinity water from the Arctic mixed with that of the World Ocean. By contrast, Kennett and Shackleton related the event to the opening of the more distant Tasman Seaway as Australia separated from Antarctica.

In western Europe the Grande Coupure is important because on paleontologically parsimonious grounds it supports the existence of a large scale basal Oligocene terrestrial dispersal event, nearly simultaneous in geological terms. It must have affected far more organisms than just the mammals and those other organisms whose fossil record possesses high enough resolution to document its occurrence. In the marine Cenozoic rocks of the world, but especially in Tethyan Europe, faunal and floral changes are marked at the Eocene-Oligocene boundary, although many taxa cross it with little or no modification (Beckmann et al., 1981; Cavelier et al., 1981; Hubbard & Boulter, 1983).

Seventeen western European terrestrial mammalian genera whose last species became extinct at the Grande Coupure, between the Ludian and the Sannoisian (= between the equivalent marine Priabonian and the Stampian, sensu lato), constitute the following list (modified from Brunet, 1977):

Artiodactyla
  Choeropotamidae
    Choeropotamus
  Xiphodontidae
    Xiphodon
    Dichodon
    Haplomeryx
  Amphimerycidae
    Pseudamphimeryx
  Anoplotheriidae
    Anoplotherium
    Dacrytherium
Creodonta
  Hyaenodontidae
    Pterodon

Primates
  Adapidae
    Adapis
  Microchoeridae
    Microchoerus
    Pseudoloris
"Insectivora"
    Amphidozotherium
    Pseudorhynchocyon
Rodentia
  Theridomyidae
    Oltinomys
    Thalerimys
    Patriotheridomys

At the same time, twenty previously unheralded new occurrences in western Europe, most of which appear to have originated elsewhere, include species of the following mammalian genera (modified on the basis of Brunet, 1977):

Perissodactyla
  Rhinocerotoidea
    Eggysodon (*Ronzotherium* and *Cadurcotherium* followed almost immediately thereafter, prior to the Ronzon Fauna)
Artiodactyla
  Entelodontidae
    Entelodon
  Anthracotheriidae
    Bothriodon
  Gelocidae
    Gelocus
Carnivora
    Amphicynodon
    Eusmilus
Insectivora
  Erinaceinae
    ?Amphechinus
  Plesiosoricidae
    Butselia
  Soricidae
    ?Quercysorex
Chiroptera
  Vespertilionidae
    Myotis (but the family was in Europe earlier)
Lagomorpha
    Desmatolagus (possibly not the same genus as the Asiatic form)
    ?Shamolagus
Rodentia
  Aplodontidae
    Sciurodon
  Theridomyidae
    Sciuromys (probably not from elsewhere, however)
  Gliridae
    Peridyromys (probably not from elsewhere, however)
  Sciuridae
    Palaeosciurus
  Cricetidae
    Eucricetodon
    Heterocricetodon

Eomyidae
Omegodus
Castoridae
Steneofiber

Passing through the western European Grande Coupure with no more than species-level adjustments were the following twenty-five lines of mammals (Brunet, 1977, with modification):

Perissodactyla
Palaeotherium
Plagiolophus
Artiodactyla
Dichobunidae
Dichobune
Cebochoeridae
Cebochoerus
Anoplotheriidae
Diplobune
Tapirulus
Cainotheriidae
Oxacron
Paroxacron
Creodonta
Hyaenodontidae
Hyaenodon
Carnivora
Canidae
Cynodictis
"Insectivora"
Nyctitheriidae
(undescribed taxon)
Talpidae
Geotrypus
Myxomygale
Pantolestidae
Dyspterna
Apatotheria
Apatemyidae
Heterohyus
Chiroptera
Rhinolophidae
Rhinolophus sensu lato
Paraphyllophora
Palaeophyllophora
Emballonuridae
Vespertiliavus
Molossidae
Tadarida
Rodentia
Theridomyidae
Theridomys
Blainvillimys
Pseudoltinomys
Elfomys
Gliridae
Gliravus

Well along in the early Oligocene, at the end of the Sannoisian (= earliest Stampian, sensu lato), between the levels represented by the late Sannoisian Ronzon and the early Stampian Villebramar faunas, another, less important event seems to characterize the western European Oli-

gocene faunal sequence. Seven mammalian lines becoming extinct at this time were:

Perissodactyla
Pseudopalaeotherium
Plagiolophus minor (a formerly long-lived species quite separate from *Plagiolophus fraasi*)
Artiodactyla
Anthracotheriidae
Bothriodon
Carnivora
Canidae
Cynodictis (may have given rise to later *Haplocyon*)
"Insectivora"
Darbonetus
Dyspterna
Cryptopithecus

Six mammalian immigrants appear to be the following:

Artiodactyla
Suidae
Palaeochoerus (perhaps earlier)
Anthracotheriidae
Anthracotherium
Gelocidae
Lophiomeryx
Hypertragulidae
Bachitherium
Carnivora
Mustelidae
Plesictis
Nimravidae
Nimravus (perhaps earlier)

Passing through the event with little more than species adjustments were thirty-nine mammalian lines:

Perissodactyla
Plagiolophus
Cadurcotherium
Eggysodon
Ronzotherium
Artiodactyla
Dichobunidae
Dichobune
Entelodontidae
Entelodon
Anoplotheriidae
Diplobune
Cainotheriidae
Plesiomeryx
Caenomeryx
Gelocidae
Gelocus
Creodonta
Hyaenodontidae
Hyaenodon
Carnivora
Amphicynodontidae
Amphicynodon
Nimravidae
Eusmilus

"Insectivora"
  Nyctitheriidae
    (undescribed taxon)
  Talpidae
    Geotrypus
    Myxomygale
  Plesiosoricidae
    Butselia
  Soricidae
    ?Quercysorex
  Erinaceinae
    ?Amphechinus
Chiroptera
  Rhinolophidae
    Rhinolophus, sensu lato
    Paraphyllophora
    Palaeophyllophora
  Emballonuridae
    Vespertiliavus
  Molossidae
    Tadarida
  Vespertilionidae
    Myotis
Lagomorpha
    Desmatolagus
Rodentia
  Aplodontidae
    Sciurodon
  Theridomyidae
    Sciuromys
    Theridomys
    Blainvillimys
    Pseudoltinomys
    Elfomys
  Gliridae
    Gliravus
    Peridyromys
  Sciuridae
    Palaeosciurus
  Cricetidae
    Eucricetodon
    Heterocricetodon
  Eomyidae
    Omegodus
  Castoridae
    Steneofiber

It is interesting as well to compare western European mammalian faunal turn-over, or rather the lack of it, at an Eocene event just before the Grande Coupure. According to Brunet's (1977) data, here slightly updated, there were few extinctions or introductions in the time immediately preceding the Grande Coupure. Thus, between the levels represented by Montmartre in the Paris Basin and St. Capraise d'Eymet in the Aquitaine Basin of France, these intra-Eocene western European mammalian extinctions were limited to the perissodactyls *Anchilophus* and several species of *Palaeotherium*. Mammalian introductions to western Europe were confined to the "insectivores" *Amphidozotherium* and *Cryptopithecus*. In a similar but more detailed

TABLE 3. Summary of western European late Eocene and early Oligocene mammals.

Time Planes	Extinctions	New Occurrences	Unaffected
Earliest/Early Stampian	7	6	39
Grande Coupure (38 Ma)	17	20	25
Montmartre/St. Capraise d'Eymet	5	2	41

study of the Paleogene mammalian faunas of Quercy, France, Crochet et al. (1981) found no dramatic breaks until the Grande Coupure. The same progressive, rather than sudden, change appears to have characterized the evolution of western European floras in the Eocene (Collinson et al., 1981). By "progressive" I do not necessarily wish to imply "gradual" or "smooth." What I do wish to indicate is that nothing spectacular occurred until the Grande Coupure.

These lists of western European late Eocene and early Oligocene mammals are summarized in Table 3.

Note that in all three levels of discernible mammalian faunal change there were more western European mammalian lineages passing through the event in situ with little or no change than the number becoming extinct. Known pre-Grande Coupure, unheralded, new mammalian additions were limited in the late Eocene to *Amphidozotherium* and *Cryptopithecus*, whose affinities are poorly understood but are not necessarily Asian or American except through remote ancestry. Of the new western European occurrences at the time of the Grande Coupure, however, nearly all had obvious Asian or American affinities or both. Exceptions or possible exceptions are the artiodactyl *Gelocus*, the theridomyid rodent *Sciuromys*, and the glirid rodent *Peridyromys*. Most or all of the new occurrences at the somewhat later earliest/early Stampian event at the end of the Sannoisian in the Oligocene also possessed Asian and/or American affinities. These new occurrences may therefore legitimately be labeled *arrivals*.

In the case of both the Grande Coupure and the later event at the end of the Sannoisian, the number of western European mammalian extinctions was about equal to the number of mammalian arrivals in each example. The Grande

Coupure, therefore, can be regarded as a biological event related to the advent of a dry-land connection from western Europe eastward to southeastern Europe and to Asia and beyond. The event is similar to what happened to South America's biota when connection to North America was established near the end of the Cenozoic (Webb, 1976; Marshall & Hecht, 1978; Marshall et al., 1982). In historical terms, it might be compared to the Oklahoma Land Rush of April 22, 1889, although I admit that fewer taxa were involved in the latter. All terrestrial organisms would have been affected, including, of course, plants, although one might suspect that many plants and some animals were able to cross the narrowing water barrier somewhat before it dried up completely. Repenning (1967) and Tedford (1970) have recommended that such biological invasions be made the basis of the beginning points of Mammalian Ages. Such a geographic change would also have had profound effects on various more distant marine environments and on climate. Indeed, the event is correlated by western European stratigraphers with the marine faunal turn-over between Priabonian and Stampian (sensu lato) faunas that is taken as the Eocene/Oligocene boundary. Cooling of oceanic bottom waters throughout the world occurred at the same time (Kennett & Shackleton, 1976), although in western Europe floristic evidence indicates that cooling of terrestrial environments had begun in the Eocene and was not particularly dramatic at the end of the Eocene (Collinson et al., 1981; but see Hubbard & Boulter, 1983). In the Arctic, however, the Oligocene temperature drop was more dramatic (Norris, 1982), suggesting as well that climatic zonation became more pronounced at the beginning of the Oligocene.

CONNECTEDNESS OF THE BERING LAND BRIDGE AREA AND THE SPECTRE OF AN ALEUTIAN BRIDGE

Although a brief stretch of shallow sea water presently interrupts land continuity between Asia and Alaska at the Bering Strait, a wide land connection formerly existed there (Scholl & Sainsbury, 1961), long before humans first used it in the Pleistocene. A dry land connection in prehistoric times has been a factor in anthropological dispersal theory since its original proposal by Fray Jose de Acosta in 1590 (Wilmsen, 1965). But, even before the Pleistocene, dry land had

apparently existed in the Bering Strait area since the Mesozoic (Hopkins, 1967; Scholl et al., 1968; Churkin, 1972), with minor epicontinental transgressions occurring at the very end of the Cenozoic (Ostenso, 1968). For a time in the 1960s and 1970s late Miocene and even earlier Cenozoic seaways through the area were postulated (Mitchell, 1966; Durham & MacNeil, 1967), but further work has discounted such early incarnations in the Cenozoic of the modern Bering Strait (McKenna, 1983, and references cited therein).

Evidently, the *utilization* of this bridge by terrestrial organisms has been controlled primarily by climate, such as warm interglacials or warm periods that extended poleward like that of the medial Miocene (Addicott, 1969) before glaciation began (Bandy et al., 1969) or the warmer climate of the early Cenozoic and Mesozoic. As can be seen from the paleomagnetic information provided by Harrison and Lindh (1982a, 1982b), the site of the Bering Strait at the end of the Cretaceous was very close to the rotational pole and the area would have suffered whatever polar climatic extremes existed then. From the late Cretaceous onward, the Bering Bridge area has steadily retreated southward relative to the rotational pole. During the early Cenozoic the Bering area would have suffered longer winter darkness and a more extreme yearly climate than any of the then more southerly placed bridges connecting Canada to Greenland and parts of Europe. The Bering Bridge area has thus long acted as a filter, sometimes strong and sometimes weak, whose action has always been controlled primarily by daylight length and climate. During the Cenozoic, only toward the close of the Era was a short Beringian water gap added to the mix.

A possible second bridge between Asia and Alaska, via the Aleutian Island chain, has been suggested by DeLong et al. (1978), who pointed out that uplift under the Aleutian arc (Gates & Gibson, 1956) would have occurred at the time of subduction of the now-destroyed Kula Ridge, which was subducted under the Aleutian Trench. The latter may have jumped southward to its present position relative to the rest of Alaska at the end of the Cretaceous (Cooper et al., 1976), or it may have had a more southerly position (Marlow & Cooper, 1983). According to DeLong et al. (1978), the present Kamchatka Strait area at the west end of the modern Aleutians originated in the late Cenozoic. Unfortunately, the

exact position or time of subduction of the Kula Ridge is not known, having been estimated as occurring either in the late Paleocene to early Eocene (Hayes & Pitman, 1970; Byrne, 1979) or in the mid-Cenozoic about 30 ± 10 million years ago (Grow & Atwater, 1970; DeLong & Mc-Dowell, 1975). DeLong et al. (1978) opted for a time of emergence beginning about 42 Ma and ending at 15 Ma. Probably any possible continuity ended before 15 Ma because the Meiji sediment tongue, directly south of Kamchatka Strait, began to form in the early Miocene (Scholl et al., 1977). Utilizing Harrison and Lindh's (1982a) paleopole positions, I calculate that at 38.9 Ma the paleolatitude of both the eastern and western portals of the ancient Aleutian arc would have been at about 63°N, with the southernmost, central part of the arc at about 58°N, provided that the arc was not farther south as suggested in one of Marlow and Cooper's (1983) models.

If an Aleutian Bridge existed, it would have filtered any exchange of organisms between Alaska and Asia because its narrowness would have allowed few biotopes and because, to cross it, organisms would have required a distribution that included the restricted position of one of its portals. The climate of such an Aleutian Bridge, however, would presumably have been somewhat milder than that of the more northerly-positioned Bering Bridge. Moreover, the length of days and nights would have been slightly more equal throughout the year. Between the two bridges, the Bering Sea might well have been a fresh-water body for a time in the mid-Cenozoic, if indeed an Aleutian Bridge was a reality and blocked water exchange with the Pacific Ocean to the south. The Sea of Japan was briefly such a fresh water body near the end of the Miocene (Burckle & Akiba, 1978). Such a possibility in the Aleutian Basin could be tested by the drill. For the moment, a mid-Cenozoic Aleutian Bridge lying to the south of the Bering Bridge is an interesting but highly speculative possibility in need of further investigation.

TECTONIC FLOTSAM

The tectonic history of the north end of the Pacific Ocean and its continental borders is becoming known rapidly, largely through paleomagnetic studies and through application of studies of the fates of the now-subducted Kula Plate and Kula Ridge as well as of the nearly

swallowed Farallon Plate (Stone et al., 1982; Jones et al., 1982) and some oceanic plateaus (Ben-Avraham & Cooper, 1981). As Pacific Ocean floor has moved thousands of kilometers generally northward, many allochthonous small blocks associated with or affected by these plates have been added to the coasts of the bordering continents or subducted beneath them (Alvarez et al., 1980; Irving et al., 1980; McElhinny et al., 1981; Barron et al., 1981; McWilliams & Howell, 1982). The history of these collisions is largely a Mesozoic one, but chunks of Alaska and British Columbia have continued to move a thousand kilometers or more during the Cenozoic (Cowan, 1982; Marlow & Cooper, 1983) and various coastal blocks of North America have rotated clockwise (Beck & Plumley, 1980; Bates et al., 1981; Globerman et al., 1982) as the result of the generally northward motion of the Pacific oceanic floor and plate consumption along the West Coast (Packer & Stone, 1972; Stone & Packer, 1977; Cox, 1980; Drake, 1982). Rotations have also been observed along the Pacific coast of Asia.

Southwestern Alaska has been the site of tectonic unrest throughout the Cenozoic as various terranes have arrived from the south (Scholl et al., 1975). Essentially all of the terranes south of the Denali Fault were formed at sites many degrees to the south of their present position and have been mashed against the North American Plate as the Kula Plate and part of the Pacific Plate moved north to destruction under North America and eastern Asia. In contrast, Paleocene volcanics just north of the Denali Fault are magnetized with steep inclinations, indicating that they were formed in high latitudes (Plumley et al., 1982). Alaska north of the Denali Fault was in essentially its present position much earlier than terranes to the south (Sweeney, 1982). Thus, environmental information derived from Paleogene and Mesozoic floras south of the Denali fault system tells us not about ancient Alaska but about somewhere else.

THROUGH THE TANK OF SHEEP-DIP

It is tempting to envision some of these far-traveled small blocks as Noah's arks (McKenna, 1973), each bearing a biota whose affinities lie with some distant homeland either along the western shore of North America or across vast oceanic stretches. Indeed, many of the blocks were in the southern hemisphere as late as Ju-

rassic times (Stone et al., 1982). However, their arrival in the north from an ultimate source in "Pacifica" (Melville, 1981; Nur & Ben-Avraham, 1977, 1981, 1982), or from oceanic volcanic arcs or mid-plate volcanic edifices that had somehow become populated from elsewhere, was in most or all cases apparently too early to have had any discernible effect on the composition of Cenozoic vertebrate faunas of the north. Further, the various blocks may not have all come from the same place. Finally, most of the blocks seem to rest on oceanic basement (Ben-Avraham et al., 1981; Jones et al., 1982) and thus those that do were never initially part of *any* continent.

Possibly the biological effects of passive transport followed by merger of the tectonic substrate could be seen by analyzing patterns of endemism of organisms whose ancestors were affected by transoceanic transfer on the fragments that have ultimately come to rest in Alaska, Siberia, Japan, or British Columbia and the western coast of the United States. Such an analysis should proceed according to the method set forth by Rosen (1978) and by Nelson and Platnick (1978, 1981). But, as I have elsewhere (McKenna, 1981) pointed out, such blocks, if embedded in oceanic crust, would tend to sink as the ocean floor moved away from a generating ridge. The amount of such sinking is generally proportional to the square root of the time involved since the site was generated at the ridge crest (Sclater & Parsons, 1981), but for most "normal" ocean floor the depth with respect to time since plate generation is perhaps better represented by the formula:

$$d = 6,400 - 3,200e^{-t/62.8}$$

where d is the depth in meters and t is time in millions of years. This formula, developed by Parsons and Sclater (1977), has the advantage of yielding results that are asymptotic to a limiting water depth of 6,400 meters. After 70 million years of lateral motion, rocks once at the mid-oceanic generating ridge subside to within about 1,000 meters of such a depth. Small blocks of continental crust, aseismic ridges, guyots, or anomalous crust such as that of the present-day Ontong Java or Manihiki plateaus (Heezen et al., 1965; Nur & Ben-Avraham, 1982; Rogers, 1982) would rise higher than "normal" oceanic floor and thus would require the use of different constants in the equation. However, if such small blocks are to be invoked as Noah's arks, it must be shown how their surfaces could have remained continuously above sea level for the en-

tire journey in order to avoid drowning their terrestrial inhabitants. Even photic zone inhabitants, for instance corals, would soon perish if in the course of their passive lateral transport they were carried to greater than shallow depths. At present, blocks like the Ontong Java, Manihiki and many other oceanic plateaus are, after all, either mostly or totally far below sea level.

Noah's Arks

Large blocks of sialic crust are another matter: we call them continents! India's northward flight away from the rest of Gondwanaland and its merger with Asia (Klootwijk & Peirce, 1979; Mitchell, 1981; Brookfield & Reynolds, 1981) is one example of a major Noah's ark transfer that was consummated some time either in the late Cretaceous or early Cenozoic prior to the medial Eocene (Maluski et al., 1982). The vicariant inhabitants of India that had resulted from its departure from other parts of Gondwanaland were largely swamped by dispersal on India's contact with Asia. Patterns of endemism that remain in India, however, point to a former Gondwana affinity of India, which is now crushed into and under the Himalayas and Tibet (Klootwijk & Bingham, 1980; Boulin, 1981; Gupta & Delany, 1981). Australia's and southern New Guinea's northward motion is well known (Wegener, 1924; Lam, 1934; LePichon & Heirtzler, 1968; Raven & Axelrod, 1974; Audley-Charles et al., 1981) and a collision with Asia is beginning (Hamilton, 1979; Coleman, 1980; Audley-Charles, 1981). South America's Cretaceous departure from Africa and its reconnection to the rest of the world via North America at the end of the Cenozoic is another example (Raven & Axelrod, 1975; Tarling, 1980; McKenna, 1980b; Vink, 1982). On a smaller scale, the many jostlings over short distances of mini- and micro-plates of the Tethyan area offer numerous possibilities for Noah's ark transfers (Scott, 1981; Thomas et al., 1982). Some of these, such as the Balearic Isles, Sardinia, southernmost Spain, Italy, Crete, and Romania, show various stages of transfer from incipient to complete (Adrover & Hugueney, 1975; Burchfiel, 1976; Leinders & Meulenkamp, 1978; Vandenberg, 1979; Cohen, 1980).

Effects of Time on Noah's Arks

A problem with invoking small, far-traveled tectonic blocks to explain transoceanic similarities or apparently embedded endemics is that

such travel in oceanic isolation takes a long time, during which significant morphologic changes may have occurred in the passively transported biota. If one accepts that a special taxonomic similarity between transoceanic sister species, genera, or families indicates former continuity of two widely separated occurrences, and one finds that fragments of a once continuous landmass upon which the ancestors of these taxa once existed are now allochthonously embedded in distant continents (Nelson, 1981), then any such taxon must independently be expected on *generally* parsimonious grounds to have existed at the time of the original fragmentation. In the case of "Pacifica" or in arguments about differential Earth expansion, this time can amount to more than a hundred million years, depending on the rate of ocean floor spreading and the distances travelled. Although it is generally recognized that the fossil record is imperfect, it is not likely that the fossil record is perverse, as some cladists would apparently have it. Thus the chances that, say, 15 discerptible sequential character states of horse evolution lasting a million years apiece actually took place in the same sequence but 15 million years earlier in each case, without leaving a record until appearing in exactly the same sequence later, unchanged, I would think to be on the order of e^{-225}, effectively equal to zero. Nor is the amphi-Pacific distribution of human populations likely to be explained by the fragmentation of "Pacifica" as is adumbrated by Nelson and Platnick (1981: 542)! Parsimony is a factor in all science, not just in the preparation of cladograms. With regard to vertebrates, I would think that only rather high-rank taxa, such as a class or subclass, might be involved (if at all) in the "Pacifica" or differential expansion scenarios. But I know of no convincing evidence that any terrestrial vertebrate lineage has been brought alive to the shores of North America from the other side of the Pacific on a fragment of "Pacifica." This is not to say that far-traveled and once submerged tectonic blocks, once they become imbedded in a new land, cannot be further transported along the edges of continents by transcurrent faulting, etc., carrying ancient fossils and newly acquired terrestrial biotas along with them to new destinations.

PLANETARY POPCORN?

That the Earth has expanded is an idea that can be traced with certainty back to the works of W. L. Green in the nineteenth century (Jordan, 1966, 1971; Carozzi, 1970; Carey, 1976). Modern metaphysical underpinnings for a form of expansion have been provided by Dirac (Wesson, 1973: Davies, 1982) although several investigators have arrived at the concept from empirical studies alone, without knowledge of Dirac's work. Possibly several different expansion mechanisms might work in concert, but appeals to unknown mechanisms should be entertained only when all else fails, as was the case in the early days of continental drift theory.

Dirac (1937, 1938, 1974) concluded inductively that there must be some connection between the gravitational "constant" and time. He, and other students since then, concluded on the basis of his "large numbers hypothesis" that the gravitational "constant" must be weakening, proportional to time elapsed since the Universe began, which Dirac believed to have been about 2 billion years. Current estimates of the age of the Universe are up to an order of magnitude greater and vary, depending on differing determinations of the Hubble constant, from at least about 10 to as much as 18 billion years (de Vaucouleurs, 1982). This gives the postulated expansion process a longer time in which to operate than Dirac originally contemplated, drastically reducing the Phanerozoic component of whatever total expansion might have occurred. That the Earth itself should have participated in Hubble expansion seems reasonable enough. Therefore, since mid-Paleozoic time, say 350 Ma, a maximum of about three percent of the Earth's expansion would have taken place. This amount is smaller than the figure given by Carey (1975, 1976), partly because his value for the age of the Universe was only about a third or a quarter of that now accepted and partly because Carey believed that the expansion accelerated exponentially with time. Owen (1976, 1981, 1983), on supposed empirical grounds that do not take into account the effects of propagating rifts, believes that the Earth's diameter has expanded by 20 percent of its modern diameter since 180–200 Ma. Steiner (1977) also believed in rapid expansion, concluding that the Earth has expanded about 11 percent since Jurassic time, an argument that precipitated a series of outcries and explanations in the June, 1978 issue of *Geology* (e.g., Kaula, 1978).

Vink (1982) and Courtillot (1982) provided models of continental rifting that effectively explain the spherical triangular apparent gores that

are the raison d'etre of attempts to match coasts or continental slopes on an Earth of smaller radius than the present one. As a rift begins to invade a continent, breaking it apart into two continents, the resulting new coasts progressively dilate and also bend down as the rift propagates. Hence the apparent gores.

Actually, what is required is not an explanation of Earth expansion. Expansion may have occurred, but, if the whole Earth expanded uniformly, then there would be no crustal separations to explain and paleomagnetic inclinations would not be expected to change. However, the Earth is not like a balloon in which the contained matter expands and the balloon itself does not. What a balloon does is to deform, thinning to the point of breakage. If a balloon truly expanded, its rubber would thicken instead of thinning as its area increased. If paleomagnetic studies were to be conducted on such a deformed, balloon-like crust, they would show modified field inclination vectors for one of two reasons. Either general crustal thinning would do the job or decrease in curvature would provide a similar result in case the continental fragments did not expand, more or less analogous to the fate of pieces of paper attached to the surface of the balloon. What is needed is an explanation of why, if general expansion has occurred and continents have separated, continental crust should not also have participated in the expansion process affecting the whole Earth, thickening as well as increasing in area. Non-expansion of part of or all of the continental crust thus is an ad hoc assumption in most scenarios. I have seen little quantitative discussion of this in the expansionist literature except that of McVittie (1969), who came to no conclusion other than that different parts of the Earth and other celestial bodies might possibly expand at differing rates at different depths. Usually, the problem is not mentioned at all.

However, if one gives proponents of substantial differential expansion the benefit of the doubt and assumes that only the Earth's core and simatic crust expanded and, as a further ad hoc assumption, that all expansion occurred between the eastern and Western shores of the Pacific, then a maximum of about 1,200 km of separation there due to differential expansion would have occurred since the mid-Paleozoic, when marine faunal similarities between Australia and North America began to drop sharply (Gill, 1958). That differential expansion was, if it occurred,

less than 1,200 km or was offset by other factors is indicated by the calculations of McElhinny et al. (1978), who concluded on the basis of paleomagnetic evidence from presumably non-expanding continents that the Earth has had a diameter within one percent of its present diameter since at least the Devonian. McElhinny and his co-workers also concluded that Mars, Mercury, and the Moon have not expanded significantly since Precambrian time. Golombek and McGill (1983) obtain similar results for the Moon.

In any case, on Earth the amount of allowed separation due to differential expansion alone would be a small fraction of the present width of the Pacific Ocean. Thus we may conclude on quantitative grounds that differential expansion, even if it were true, would not help much in the field of paleobiogeography except to increase the degree of some ancient separations by a small amount. Far more important is the fact that the floor of the Pacific is decoupled from its surrounding continents and the size of the Pacific Ocean itself has been shrinking, not expanding, since the time of the Pangaea assembly. Sea floor created is eventually subducted. An area of the ocean floor equivalent to that of the present Pacific Basin has been subducted since early Cretaceous time alone (Larson & Pitman, 1972), and there is ample evidence that the process was ongoing long before that. Such processes have been recycling sediments derived from the continents into the mantle since Precambrian time (DePaolo, 1983).

Recently, however, Nelson and some other students of vicariance biogeography have been impressed by non-quantitatively assessed accelerated expanding Earth models, evidently as a means of explaining amphipacific organismic distributions without recourse to dispersal or to vicariance dependent on currently accepted plate tectonic reconstructions (Nelson, 1981; Nelson & Platnick, 1981). As did Hilgenberg (1933), Halm (1935), Brosske (1962; see Jordan, 1971), Barnett (1962), and Meservey (1969), they obtain a direct route across the Pacific (Panthalassa) by simply removing the Pacific Basin, juxtaposing its sides by postulating a much smaller former Earth on which the continents somehow retained the same area as now, covering essentially the whole surface of the Earth. This superficially attractive solution does not adequately address several questions: 1) where and how deep the ocean water of the world was previously, 2) what is to be done with abundant geological evidence

that an ocean has existed in the Pacific area, for instance off North America's west coast, since the early Paleozoic or Precambrian (Roberts, 1972; Cook & Taylor, 1975; Badham, 1978, 1979; Hoffman, 1979), 3) how 304–311 million year old ophiolites in California (Saleeby, 1982) or Ordovician ophiolites further north (Churkin & Eberlein, 1977) are to be explained, or 4) how evidence of pre-Pangaean Wilson cycles like that of the Iapetus Ocean are to be discounted (Glikson, 1972)? Such an Earth would necessarily have expanded differentially at a much greater rate than is required by Dirac's inductive insights, more or less like a piece of cosmic popcorn. If caused by Dirac's mechanism, however, the expansion envisioned would clearly be evidence that the Universe is much younger than the current consensus would have it. Thus, one might conclude that, if proponents of accelerating expansion are correct, all physics should adjust itself in some major way to their requirements (Kaula, 1978; Steiner, 1978).

But, perhaps supporters of the supposed biogeographical explanatory power of the differential expanding Earth hypothesis have erred in not going far enough. Generalized tracks (Croizat et al., 1974) are drawn between landmasses in such a way as to occupy the shortest distance between them. So the most direct route from Australia to the Americas is actually *through* the Earth, not along its surface. Such a tunnel would do less violence to the models of hopelessly complacent physicists and geologists than would an accelerated expanding Earth model in which, in terms of the model, continents are gratuitously assumed to have remained of fixed area and thickness. If students of transoceanic Pacific vicariance are willing to stretch generalized tracks so that they fall on the Earth's surface rather than within the Earth, why are they unwilling to stretch the tracks so that they go around the Pacific rather than through it?

Against a backdrop of general parsimony and in the absence of a quantitative expansion model, I cannot take the accelerated expanding Earth model seriously as a source of discernible late Phanerozoic biogeographical pattern. For such purposes, either linear or accelerated expansion has been investigated and has been found wanting. Those who disagree should seek a flaw in the arguments presented by Van Andel and Hospers (1969), McElhinny (1973), McElhinny et al. (1978), and Golombek and McGill (1983). Carey (1975) has done so with regard to the arguments

of Van Andel and Hospers, but, insofar as I know, McElhinny's work has not yet been seriously challenged, even by Owen (1981, 1983).

IMPACTS OF APOLLO-CLASS ASTEROIDS AND COMETS

Recently, the possible effects of impacts with the Earth of Apollo-class asteroids and comets have been much discussed (e.g., Napier & Clube, 1979; Emiliani, 1980; Alvarez, 1982; Alvarez et al., 1982; Clube & Napier, 1982). Although such impacts are well correlated with extinctions of calcareous marine microplankton, there is as yet no convincing evidence that these events always correlate with major terrestrial turn-over. At the Cretaceous-Tertiary boundary the effect of an Apollo-class bolide on large terrestrial organisms, such as the last surviving dinosaurs, was apparently nearly synchronous at the power of resolution studied (Russell & Singh, 1978; Russell, 1979; Hickey, 1981; Clemens et al., 1981; Archibald & Clemens, 1982; Archibald et al., 1982; and, especially, Alvarez, 1982, for statistical analysis).

Later, supposedly at 34.6 ± 4.2 Ma (Glass & Crosbie, 1982), another major impact, the cause of the North American tectite strewn field, has been widely discussed. But at 35 Ma there was no especially pronounced terrestrial vertebrate faunal turn-over. Prothero (1982) has noted a minor vertebrate faunal turn-over at 32.4 Ma, but this followed a period of stasis after a major faunal turn-over in the interval from 40 to 37 Ma Keller et al. (1983) give convincing evidence that the North American tectite strewn field occurred at 37.5–38 Ma in the latest Eocene, not later as suggested by fission track age determinations or those based on glauconite. Keller et al. (1983) also found evidence of at least two other tectite strewn fields at about the Eocene/ Oligocene boundary, but no mass extinction was associated with any of them.

Recent attempts to correlate the supposed event at about 35 Ma with the Eocene-Oligocene boundary (Glass & Crosbie, 1982) or presumed equivalent boundaries between marine invertebrate or North American mammalian biostratigraphic units have simply ignored abundant high temperature K-Ar dates from volcanic rocks interlayered with fossil bearing sediments whose paleomagnetic stratigraphy can also be studied. These dates calibrate Uintan-Duchesnean-Chadronian faunal and floral turn-over (Leopold & MacGinitie, 1972; Wilson, 1980) in North

America as occurring close to 38 Ma (Berggren et al., 1978) or 36.6 Ma (Berggren et al., 1982; in press). Prothero et al. (1982) come to similar conclusions. Nor could an impact at a later date explain the flood of Asian and/or American arrivals that characterized the Grande Coupure in Europe. In Europe the Grande Coupure has been dated at 37–38 Ma (Gramann et al., 1975; Van Couvering et al., 1981). Iridium-rich layers incorporating undifferentiated Solar System matter are indeed associated with some (but not all) large Cenozoic impacts, but if one hypothesizes that large-scale effects on terrestrial biotas have occurred through the agency of a particular bolide, one should provide clear evidence of simultaneity. This has not yet been produced. Meteoric dust has of course long been known to be a component of the Earth's sediments (e.g., Skolnick, 1959). Moreover, more biological evidence than the extinction of five species of radiolarians (Glass & Crosbie, 1982; Ganapathy, 1982) needs to be associated with the supposed 35 Ma single event if it is deemed to be especially important. Radiolaria were little affected by the impact that occurred in close association with the Cretaceous-Tertiary boundary (Emiliani et al., 1981), so it is unclear whether a causal relation exists. Microtectites and iridium anomalies should be sought throughout the geologic column before those few that are known now are specifically assigned far-reaching importance as evidence of extraterrestrial impacts of sufficient magnitude to have served as forcing factors in the biological world. Already, there appear to be several candidates among the various known large terrestrial impact craters (Hughes, 1979) to be the sources of at least three different Late Eocene and/or Oligocene strewn fields of tectites (Bottomly et al., 1979; Keller et al., 1983). It is equally clear from Hughes's (1979) map that many unrecognized impact structures remain to be found in non-subducted ocean floor. How many more have been lost to subduction is unknown.

EFFECTS OF RADIOISOTOPIC CALIBRATION ON TEMPORAL DISTRIBUTION

Most of this essay has been concerned with spatial distribution, but recent discussions of rates of extinction and of faunal turn-over (Flessa, 1975; Raup & Marshall, 1980; and other articles on the same general subject in the journal *Paleobiology*) prompt a few brief comments about the obvious but nevertheless seem necessary. A

first point is that compilations should be based on specific lineages, not on higher taxa. Technically, it is not genera, families, orders, etc., that originate, evolve, or become extinct. For example, it is the perishing of the last species of a higher taxon that causes the higher taxon to perish. Discussions of the sudden extinctions of higher taxa may well mask a series of more gradual extinctions of various genetically isolated lineages within any particular higher taxon. Studies of extinction, to be convincing, need to discuss the relative abundance and presence or absence of taxa at the species level and to relate this information to measured stratigraphic sections studied in the field rather than to derive their basic information from popular texts such as Romer's (1966) Vertebrate Paleontology.

A related point has to do with rates of faunal change. For these to be calculated, some form of temporal calibration is required, of which the most effective one is a time scale measured in years. Such a calibrated time scale is not yet available for much of the fossil record, at least not at the power of resolution necessary for detailed study. What generally happens instead is that biostratigraphically-based time divisions within a particular interval are treated as aliquots (Fig. 1). The abundance of taxa within these units is assumed to be meaningful, but instead the diversity of a longer interval could be caused by mixing the diversity of two or more unrecognized levels within the unit. This has been demonstrated, for example, in the case of the long North American Wasatchian and Uintan Land Mammal ages relative to the much shorter Bridgerian Land Mammal Age (Berggren et al., 1978). The apparently high diversity of some units given aliquot status in biostratigraphy may be caused simply by their long duration and therefore by their temporally composite sampling of the passing kaleidoscope of life (Raup & Marshall, 1980) (Fig. 2).

EXTENSIONS OF SIMPSON'S BIOGEOGRAPHIC PRINCIPLES

Simpson (1940a, 1940b, 1943, 1952, 1953, 1965) developed the notions of biogeographic corridors, filters, and sweepstakes (McKenna, 1975). Basically, these constitute a spectrum of permissiveness with regard to dispersal and possess statistical signatures when sampled in the geological record. Provided the record is adequate, one should in principle be able to recog-
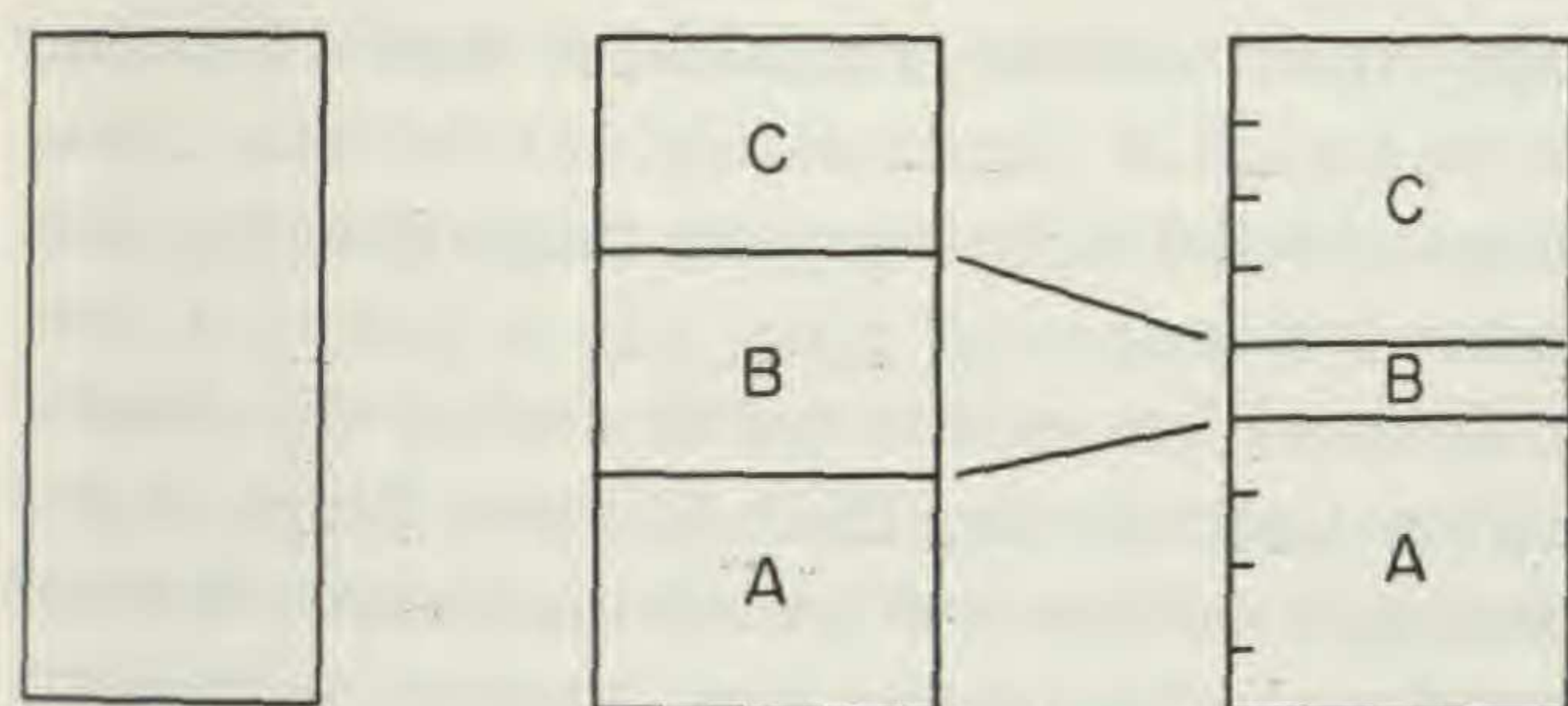
FIGURE 1. As biostratigraphic units are recognized, they tend to be given aliquot status. Although their temporal sequence is known, the temporal duration of units A, B, and C is not at first known but is later calibrated.
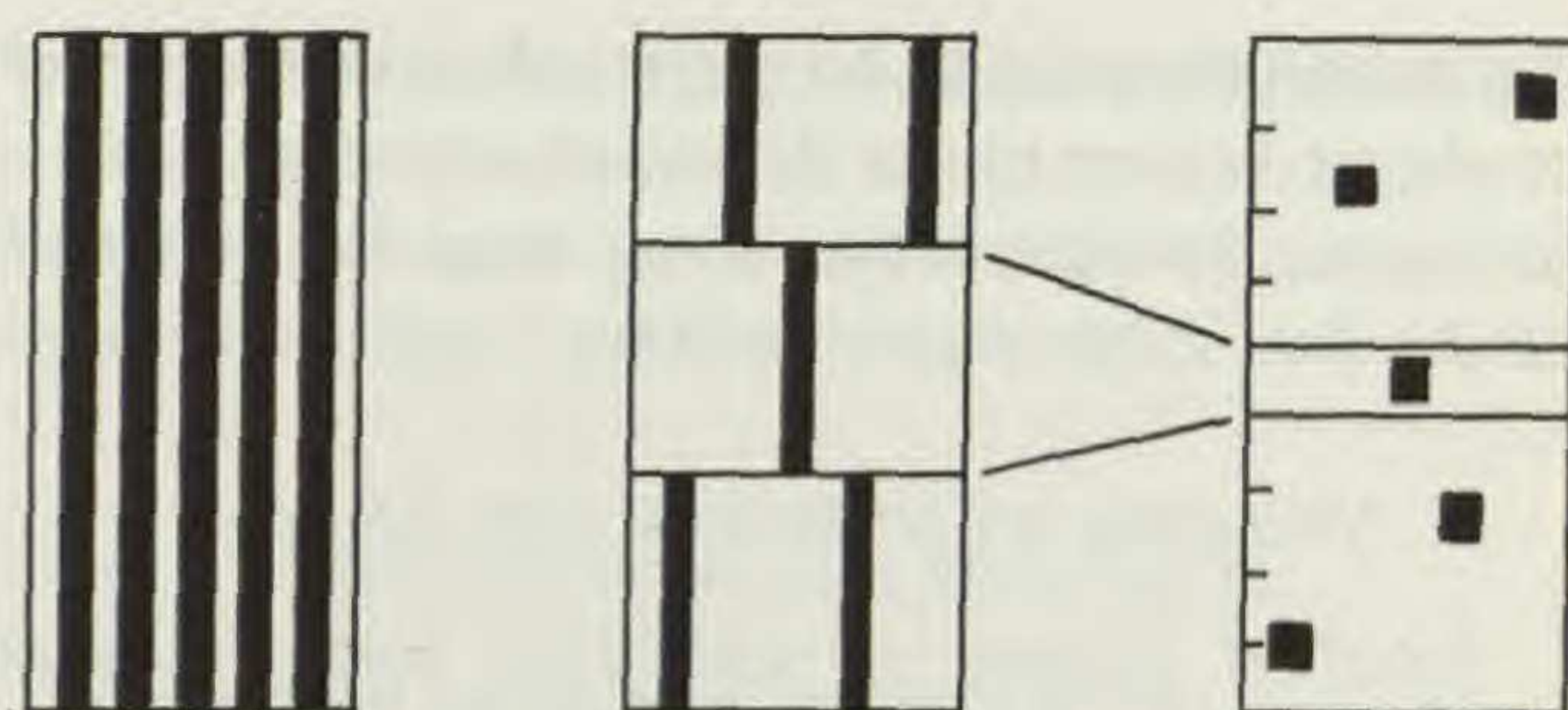
FIGURE 2. Before biostratigraphic subdivision, the biological diversity of a sequence of rocks is merely known to occur in the sequence (left). Upon biostratigraphic subdivision into aliquot parts, the diversity of known fossils within the aliquots can be compared and may be found to differ (center), leading to estimates of rates and intensity of various evolutionary phenomena. When the duration of the biostratigraphic subdivisions is provided by temporal calibration (right), the apparent diversity of units of long duration may turn out to be better interpreted as the result of mixture of sequential diversities that are themselves relatively constant. Previous estimates of the evolutionary processes involved may turn out to have been in error.

nize when two areas were connected to each other by a continuously habitable substrate, when the substrate was partially a barrier, and when the barrier was more complete as in the case of random over-water transport of organisms to islands. Assuming the imperfect geological record of organisms to stop short of perversity, one can assess the extinct biotas of various landmasses of the Earth and make reasonable estimates from biological resemblances whether certain land areas were freely accessible to each other's biotas. Simpson based his arguments on the stable-continent rationale and most of his examples are drawn from fossil mammals. However, his principles are adaptable to a mobilistic world and are still valuable in spite of criticism of past excesses by Du Toit (1944), and in spite of simple avoidance of discussion of them by most vicariance biogeographers.

There is no need to repeat all of Simpson's arguments here, but suffice it to say that terrestrial corridors are defined when biological resemblances between two distant samples are approximately the same as would be found at present between samples drawn from opposite sides of a continent, say Eurasia or North America. If a corridor came suddenly into existence, dispersal would be in both directions and would not be long delayed. Ecologically balanced biotas would be involved. At the other end of the spectrum, sweepstakes dispersal would be characterized by random arrivals, one-way transfers, ecological imbalance, and delayed introductions. In between would be various types of filters that permitted some but not all organisms to pass. Simpson discussed this spectrum as though its components represented separate processes, but in a mobile world it is especially obvious, for instance, that whole oceans were once inches,

then feet, then miles wide. At certain points in this progression the statistical properties of Simpson's corridors, filters, and sweepstakes would each have helped to shape the evolutionary history of the biotas involved.

Because of the stabilist rationale implicit in Simpson's earlier work, Simpson believed one-way transfers of balanced biotas to be unlikely. To be fair, it should be noted that Simpson did toy with the idea of one-way or "revolving-door" transfer by means of sequentially uplifted and then subsided blocks, thus avoiding large-scale horizontal displacements such as those contemplated in present geological thought. However, under a mobile rationale such transfers are possible passively, as the result of motions of parts of landmasses to join others. As have many others, I have elsewhere (McKenna, 1975) called the substrates on which such one-way transfers take place "Noah's arks." A related concept dealing with fossils is that of "grounded Viking funeral ships" (McKenna, 1975). The idea here is that fossils, as well as living organisms, can be carried by moving crust and added to other landmasses by the process of continental accretion, as has been demonstrated for North America's west coast (Jones et al., 1978). The difference is that the fossils that come to be imbedded in a new host landmass do not stray from their resting places to infect the rest of the landmass's biota. Like transferred fender paint in an automobile collision, they reflect only former allegiances.

Such transfers are to be expected as the result of multiple Wilson cycles that open and close oceans and, on a smaller scale, along large transcurrent faults that cross water barriers.

VOYAGES TO NOWHERE AND RETURN

Another feature of mobilistic tectonics that permits some additional embroidery of the theme that plate tectonics supplies mechanisms undreamed of in stabilists' philosophy is the phenomenon of back-arc spreading. This results in the separation of an intracontinental volcanic chain, such as the Andes or Cascades, to become an offshore arc that may later be driven back against the same continent from which it originally separated. Japan is undergoing this process (Uyeda & Miyashiro, 1974), and a similar process affected the southern Andes in the past (Dalziel et al., 1974; Dalziel & Palmer, 1979). Such separations occur because the cooling of sinking slabs of oceanic crust sometimes results in seaward jumps of subduction zones. This is because, in effect, the whole slab sometimes pulls away from the surface at a point closer to its generating ridge than the point of its earlier subduction. The volcanic arc behind the subduction zone therefore moves offshore. Continued subduction under an advancing continent would result in the arc's rejoining the continent unless another seaward jump of the subduction zone occurred in time (Uyeda, 1981). During the time that such an island arc was in isolation, both vicariance and dispersal followed by differentiation would produce peripheral isolates in abundance. Then these would be merged with the biota of the mainland. Much diversity could be created in this manner, but there could be a substantial time delay before re-introduction to the mainland.

Voyages to nowhere and return are not the result of simple intermittent barrier erection and destruction such as might be envisioned in the case of coastal islands created by eustatic rises of sea level, followed by a fall. They involve passive separation and physical removal of a biota to a significant distance on a moving substrate, followed by return and passive merger.

ESCALATOR COUNTERFLOW

Everyone has seen children turn escalators into treadmills by walking counter to the expected flow of traffic. As long as the child walks at the same speed that the escalator maintains in the opposite direction, the child remains stationary with regard to the escalator's foundations. What does this have to do with biogeography? Consider Iceland.

Iceland lies at the north end of the Atlantic Ocean, astride the Mid-Atlantic Ridge. It is a volcanic edifice built above a hotspot that has produced abnormally large volumes of lavas episodically and variably throughout most of the Cenozoic (Schilling et al., 1982). The oldest rocks on Iceland are known from coastal areas in the eastern and northwestern parts of the island, where they are about 16 million years old (Moorbath et al., 1968). Fossil plants and insects are known from late Tertiary volcaniclastics in northwestern Iceland, but as yet no fossil mammals have come to light. Geologically, Iceland is a steady-state phenomenon, in that its land spreads from the center above the hotspot and sinks below sea level after about 15 or 20 million years of lateral transport. Thus the main subaerial part of the Icelandic lava pile has covered more or less the same area of crust for a long time (Vogt, 1972). Early in the Cenozoic, early Iceland rose up to choke the whole North Atlantic for a time, creating a land bridge from Greenland to Scotland. Later, as the North Atlantic widened, Iceland came to be partly and then wholly isolated.

Apparently, Iceland retained its connection with Greenland and thence to North America longer than it did with Scotland (Friedrich, 1966; Grønlie, 1979). In the Miocene, Iceland still supported species of *Magnolia, Liriodendron, Juglans, Betula, Acer, Abies, Ulmus, Sequoiadendron, Sassafras, Populus,* and *Picea,* as well as a species of the hickory aphid *Longistigma* (Heie & Friedrich, 1971). Their respective closest species-level relatives at the time were in North America rather than in Europe (Friedrich & Simonarson, 1981). It is not yet known when these organisms *first arrived* in Iceland. At present, however, after the glacial events of the Pleistocene and subsequent repopulation of most of the flora by various means, Iceland's flora is primarily European in character (Einarsson, 1963).

New subaerial crust has been more or less constantly created at the generating plate boundary that crosses central Iceland, separating the growing Eurasian and North American plates. Because the Icelandic hotspot is associated with the plate boundary and because abnormally large volumes of volcanic products are brought to the

surface, Iceland is subaerial rather than just another part of the Mid-Atlantic Ridge. About 20 million years after any particular batch of new crust is created at the plate boundary over the hotspot, the crust will have been moved aside because of the creation of still newer crust at the boundary, eroding at the surface and cooling and subsiding to sea level and below as it spreads at a rate of about one centimeter per year. After sinking beneath the waves, 20 million year old or older Icelandic volcanics on either side of Iceland simply become parts of the submarine Greenland-Scotland Ridge.

The land surface of Iceland at any particular time thus comprises two "down" escalators arranged back to back, whose oppositely directed lateral components of motion start at the plate boundary in the middle and continue to the ocean on opposite coasts. To have escaped drowning, the terrestrial biota of Iceland merely needs to have moved over the land surface toward Iceland's central volcanic zone at a rate of about one centimeter per year for as long as the hotspot has maintained Iceland as an island above sea level (Fig. 3). Subaerial Iceland began to form at about the time of marine magnetic anomaly 24, at about 54 Ma, and appears to have remained connected to Greenland until some time in the Miocene. It might therefore be expected that Iceland once possessed a biota (prior to its being almost entirely snuffed out by glaciation) whose origin from a continent could have been, except for later dispersals, earlier than the oldest rock now present above sea level in Iceland (McKenna, 1983). Twenty million years from now, after Iceland's present rocks have moved beneath the Atlantic, some of the members of the present Icelandic biota may still be there on Iceland's newest crust, slowly climbing up "down" escalators.

Thus, it is permissible to generalize that steady-state islands lying over volanic spreading centers can have biotic components that are significantly older than the oldest rocks now present either at the island's surface or located directly underneath. Such ancient terrestrial components can have been continuously in residence on dry land for a length of time that need not necessarily be limited by the age of the oldest known insular rocks but may instead date back to the beginning of hotspot activity. An important way to test such a possibility would be to compare the hotspot age with the known geologic ranges of closely related sister taxa occurring elsewhere in the world. Obviously, taxa in passive isolation on evolving hotspots must be as old as the hotspot's isolation or must have arrived by dispersal at some later date.

HOPSCOTCH ON THE ESCALATOR

A potential mode of distribution that is in some ways intermediate between vicariance and dispersal is apparently represented well by the Hawaiian Islands and perhaps by other mid-plate hotspot edifices (Axelrod, 1972).

Vicariance, it will be remembered, results when a barrier arises *after* a distribution of organisms has been established, breaking it apart into isolated sister taxa (Croizat et al., 1974: 277–278; Nelson & Platnick, 1981). One way, but certainly not the only way, to cause vicariance is to pull apart the passive riders on two differentially moving tectonic plates. Dispersal, on the other hand, crosses *pre-existing* barriers to establish a new, expanded distribution, but processes such as the founder effect and difficulties of passing through the same barrier in the opposite direction (if, say, oceanic currents are involved) allow differentiation of sister taxa after dispersal occurs. Further, dispersal is an active process whereas vicariance brought about by tectonic plate motions does not require movement above the substrate on the part of the participants. Both processes may be responsible for the origin of biotas, particularly those of islands.

The Hawaiian Islands are collectively a long term steady state phenomenon, like Iceland, but, in contrast to the latter, the Hawaiian chain is not located on a mid-oceanic ridge nor has it recently been connected to any continental mass (Jackson et al., 1972; Dalrymple et al., 1973; Dalrymple et al., 1981). Both places are the result of subaerially produced hotspot lavas; but in the case of the Hawaiian chain, the Pacific Plate, which currently underlies the chain, is moving with respect to the hotspot and thus carries away the volcanic piles generated by the hotspot. The hotspot itself has moved relatively little, if at all, with respect to Earth's spin axis since Cretaceous time (Hammond et al., 1979; Suarez & Molnar, 1980; Gordon & Cape, 1981). At present the sea floor of the Pacific Plate in the Hawaiian area is moving west-northwestward over the Hawaiian hotspot, passing it by (Wilson, 1963) and carrying formerly tropical islands northwestward into cooler waters (Greene et al., 1978). How-
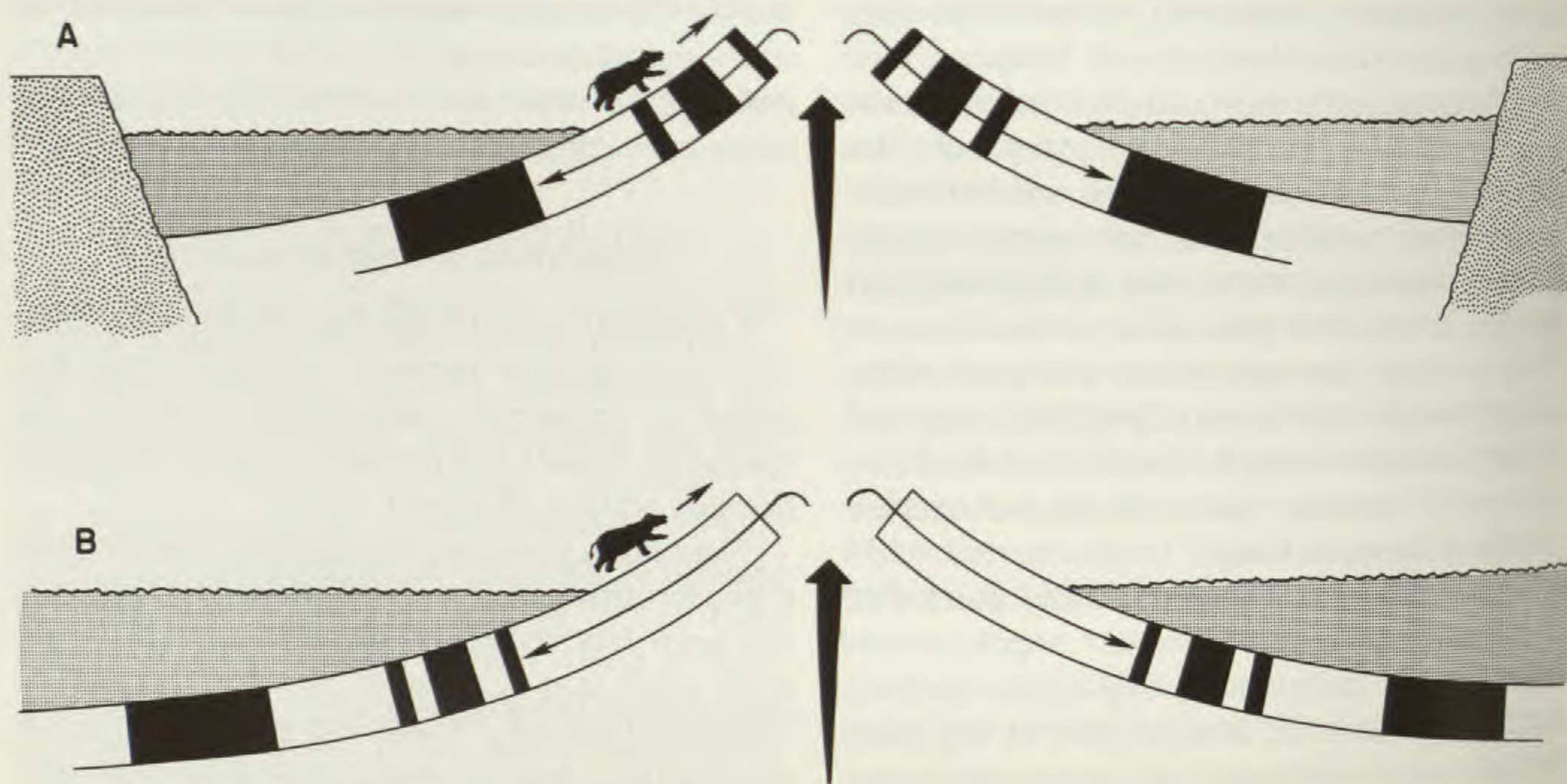
FIGURE 3. Escalator Counterflow. This cartoon attempts to show two stages in the geologic history of a mid-ocean ridge volcanic island such as Iceland. A: New crust rises from the underlying hotspot and spreads in opposite directions from the plate boundary. Magnetic polarity reversals are recorded in the volcanics as they solidify, resulting in a recognizable pattern that is symmetrical with regard to the plate boundary. Separating continents are still nearby, but the island is now surrounded by deep water, whereas it once choked the incipient ocean between them when sea-floor spreading had just begun. To avoid a salt water bath, the island's biota must move toward the plate boundary at the same rate that new crust is created—perhaps a centimeter or a few centimeters per year. B: After some time (shown by the retreat of the recognizable magnetic polarity pattern), the island is still there, although composed of younger crust. The separating continents are now no longer near, but the biota could still be present, evolving in isolation and being winnowed by extinction as well as added to by occasional arrivals from elsewhere. Thus, it is possible that some island biotas either have or have had composite mixtures of lineages that arrived both by dry land and by the various agencies of transoceanic dispersal.

ever, the rising magma column is not constantly beneath a weak plate boundary as is the case with Iceland. Rather, the column must bend as the plate passes overhead, occasionally breaking and reestablishing a more direct route to the surface. Every so often magma breaks through the plate from below to form new volcanoes above, but these form generally at the southeast end of the Hawaiian chain, first as submarine volcanoes (Emery, 1955) and then massive subaerially projecting structures as they grow in size. Indeed, one is forming beneath the surface of the ocean at present, southeast of the Island of Hawaii at Loihi Submarine Volcano (Klein, 1982; Malahoff et al., 1982). Some of the individual volcanoes in the Hawaiian chain reach a height of 9,000 meters above the sea floor, projecting up to about 5,000 meters above sea level. Meanwhile, the crust to the west-northwest cools as it departs the vicinity of the hotspot. Gradually it sinks and the older volcanic piles lying on it erode (Fig. 4). Eventually they sink beneath sea level (Vogt & Ostenso, 1967). The oldest islands of the Hawaiian chain are therefore located in the

west-northwest, as J. D. Dana realized as early as 1849 and as was finally demonstrated by potassium-argon dating more than a hundred years later (McDougall, 1964). Several volcanic piles in the chain may have been present on the Pacific Plate before their sites passed over the hotspot, however. Wentworth Seamount and Necker Island have yielded Cretaceous K-Ar ages (Clague, 1975). Rotondo et al. (1981) have discussed the possible biological consequences of adding these edifices to the Hawaiian chain.

The sporadic nature of the hotspot vulcanism results in gaps between the islands, but these are not very great in most cases. Islands that are initially separate may join as the volcanic piles enlarge. The combined Hawaiian-Emperor chain contains 107 or more recognized volcanoes (Bargar & Jackson, 1974).

The Hawaiian process has been going on like this for a very long time. About 43 million years ago the present WNW motion of the Pacific Plate began (Dalrymple et al., 1977; age corrected for currently accepted decay and abundance constants). During the early Cenozoic the motion of

FIGURE 4.   Hopscotch on the Escalator. Based on the model provided by the Hawaiian Islands, it is possible to envision a situation in which new islands arise at one end of an island chain while others sink at the other end. Some new islands would coalesce, but others would be separated by short water gaps. This process could go on for a very long time and islands (not necessarily the same islands) would have been continuously present during that time. Rocks on any particular island now above sea level would be very young, but that would not mean that the biota of the islands had necessarily arrived in the islands recently or that all members of the biota would have had to cross whatever oceanic barriers now isolate the islands from other landmasses. Dispersals among and to the ongoing sequence of islands could have occurred over a very long time and truly ancient inhabitants might be present that had never had to cross more than minor water barriers in order to be present on at least one island at any particular time. If the hotspot were old enough, it would probably once have been beneath a continent. Thus some terrestrial endemics might have arrived across barriers less stringent than those usually postulated in the biogeographical literature.

the western part of what is now the Pacific Plate (Izanagi Plate of Woods & Davies, 1982) was more nearly northward because of the action of the Emperor Spreading System, but prior to about 67 Ma. Pacific Plate motion was also west-northwestward (Farrar & Dixon, 1981; but see Gordon, 1982). The trace of the Hawaiian hotspot on the present-day Pacific Plate turns northward at Yuryaku Seamount (Long. 172°E, Lat. 33°N), where it continues as the Emperor Seamount chain (Morgan, 1972). Basalt dredged from Yuryaku Seamount has an age of about 43 Ma (Clague et al., 1975; age corrected). One of the most southerly of the drowned volcanoes of the Emperor chain, Koko Seamount, has an Eocene age of about 47 Ma on the basis of K-Ar methods (Clague & Dalrymple, 1973; age corrected) and may be slightly older than that on the basis of nannofossils of the *Discoaster lodoensis* Zone from its sedimentary cap (Moberly & Larson, 1975). The Emperor Seamount chain extends as a string of drowned volcanoes as far as the present edge of the Pacific Plate, where Cretaceous forerunners of Hawaii, now mere guyots, are being consumed in a cusp between the two curved oceanic subduction zones at the Aleutian and

Kurile trenches. Meiji Seamount at the north end of the presently available Emperor chain is about to be subducted there. The oldest fossils from sediments on Meiji Seamount (DSDP Site 192) are at least 70 million years old (Scholl et al., 1971) and are of near tropical organisms. By Oligocene time Meiji had moved north far enough to encounter subarctic conditions (Scholl & Creager, 1973). How long before the beginning of the Cenozoic "Hawaiis" older than Meiji Seamount were being created, transported, subsided, and eventually consumed is not known because of the unfortunate habit of subduction zones to obliterate direct evidence. Nevertheless, a large number of previous Hawaiian-Emperor Islands may have been subducted because the consuming arc systems have apparently become choked long enough to form the cusp between the arcs. The Hawaiian hotspot and its fossil trail of mid-oceanic lava piles could even have already been in existence before the beginning of its presence under the Pacific Plate. It is conceivable that truly ancient versions of Hawaii could have formed in contact with or even on top of a continent that happened to be passing over the hotspot.

For this reason, it is possible to envision a constant winnowing process that would result in erratic distributions within the subaerial part of the chain as terrestrial organisms were forced to play the children's game of hopscotch in order to survive. As new islands formed at one end of the chain, others were sinking at the opposite end. Thus, as with Iceland, the terrestrial fauna and flora of the present-day Hawaiian chain may well be derived, not necessarily totally from long-range over-water transport but rather at least in part from an early vicariant event followed by a series of short dispersals (Axelrod, 1960, 1972). The average distance between volcanoes along the Hawaiian chain is about 56 km; in the Emperor chain the average is about 77 km. Such distances would not be difficult for many insects or flowering plants to cross, as for instance appears to be the case in the Solomon Islands (Whitmore, 1973) or near Puerto Rico (Heatwole & Levins, 1972) at present.

Although the rocks of any particular island still above sea level in the present-day Hawaiian chain are very young (Zimmerman, 1948), the ancestors of some of the present inhabitants of the island may have been living in precarious mid-oceanic isolation for more than a hundred million years. Authors steeped in a stable continent rationale, like Zimmerman (1948), Carlquist (1974, 1982), or Carson (1982) were unable to appreciate this mobilist notion. This is because the Hawaiian chain, like Iceland, is the result of steady-state phenomena. As new Hawaiis are created, old ones sink beneath the waves to the northwest of the string of lava piles created by the Hawaiian hotspot on the Pacific Plate as the latter moves northwestward over the hotspot. Thus, arguments for rapid evolution of Hawaiian *Drosophila* (e.g., Carson, 1976; Kaneshiro & Ohta, 1982) may in some cases overestimate evolutionary rates of species origin by as much as two orders of magnitude. The apparently very ancient arrival in the Hawaiian Islands of primitive land snails that so puzzled Pilsbry (1900, 1916) or of those from the lower Miocene of Bikini in the Marshalls (Ladd, 1965) may indeed be real and permitted by the hotspot history of the areas. Even dispersals to the islands from far away could have been taking place over a much longer time span than that represented by the oldest presently exposed rocks of the Hawaiian Islands, thus helping to explain the differentiation of birds like the Hawaiian finches (Hawaiian honeycreepers), various flightless geese, rails, and an ibis, three species of an extinct genus of owls,

and still other endemic birds that occur in fossil deposits of Kauai, Oahu, Molokai, and Maui (Olson & James, 1982).

Obviously, the longer the winnowing process went on, the greater would be the probability of extinction of any original vicariant lineages and the more erratic in taxonomic composition would be the remaining sample of original terrestrial immigrants or early dispersals to Hawaii or other hotspot islands. In the Pacific Ocean alone there are many potential examples of the process, such as the Tuamotus and their symmetrically related Nazca Ridge counterpart, the Austral-Cook chain, the Easter-Sala y Gomez chain, the Juan Fernandez seamount chain and Juan Fernandez itself, the Galapagos-Carnegie Ridge area and Cocos Ridge. However, the Line Islands may not have been generated by a hotspot of the Hawaiian-Emperor type (Haggerty et al., 1982). I have argued here, however, that on geological grounds it is by no means mandatory to conclude that all inhabitants of presently isolated hotspot island groups arrived by relatively recent long-distance dispersal over water or necessarily had ancestors that did so. Rather, a series of short dispersals, carried out over a long time, may explain the existence of some of the taxa present. Original terrestrial immigrants and arriving products of over-water dispersal alike would be potential players of hopscotch on their moving substrates from the moment they began residence over a hotspot.

Clearly, in the case of some island groups, the theory of island biogeography as developed by MacArthur and Wilson (1967) is in need of modification. Olson and James (1982) have already noted this with regard to the avifauna of the Hawaiian chain because of the recent realization that the extinct endemic avifauna was more than twice as diverse as the present one. The effect of a winnowing action over a long period of time also needs to be taken into account in future work because winnowing would produce the same results as are generally attributed to the sporadic agencies of long-distance dispersal.

CLOSING NOTE OF CAUTION

In this paper I have tried to list some geological processes that might help to explain some biological distributions in space and time. I have tried also to review some extraterrestrial and even cosmological causes that might influence these distributions either directly or indirectly. As a result, I have been led to discount theories of

mean spin axis stability change, the "Pacifica" concept as an explanation of discernible Cenozoic biogeographic pattern, and accelerated differential Earth expansion as a similar explanation. I have also taken the view that "what is good for mammals must be good for everybody," but if the conclusions based here on geology and on mammals are tested and found wanting on the basis of studies of other organisms, then progress will have been made. Inasmuch as the paper was prepared for a botanical symposium, it will be interesting, at least for me, to see if the geological processes discussed here lead to any new insights regarding the floras of various parts of the Earth.

I must caution the reader, however, not to just accept the dictates of plate tectonics in place of analyzing geology and biology separately in order to preserve mutual testability. It is curious how willing some biologists are to believe the geologists, yet there is a far smaller flow of information in the opposite direction. Few geologic papers cite biological attempts to work out paleogeography, although Wegener did not hesitate to do so. Probably this is because the efforts of the biologists have not seemed to be very rigorous or quantitative to geologists and geophysicists. Mammalogists, geologists, and, yes, the botanists, need to analyze their data by means of the cladistic methods developed recently by vicariance biogeographers and also by the more classical and statistical methods of Simpson, the latter stripped of their stabilist shortcomings and amplified by the addition of some new effects generated by mobilist geology. There are dangers of circularity and non-testability if one incorporates data too early that should first be used as tests, but, once that phase is completed, synthesis is in order.

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NOTE ADDED IN PROOF: While this paper was in press, the book *The Expanding Earth, A Symposium* (Symposia of the Geology Department, University of Tazmania, no. 6, 1981, 213 pp.) was brought to my attention. The Symposium contains 54 articles, many of them strongly in favor of earth expansion of one sort or another and opposed to large-scale subduction. I do not find the arguments presented in these papers convincing, and therefore see no reason to modify statements made above. In a quantitative contribution to the Symposium, A. D. Stewart strongly bolsters the conclusions of McElhinny, Taylor, and Stevenson (1978) that the Earth has not changed appreciably in radius since the Paleozoic.